Is Fixed Action Pattern a Useful Concept?

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ABSTRACT

In this chapter, the concept of "fixed action pattern" (FAP) ("Erbkoordination"), as developed by K. Lorenz, as well as its past and present interpretations are presented. The fate of the FAP concept in neuroethology and its emergence with other concepts—the feature-detector concept, the command neuron concept, and the central pattern generator concept—is described. Two "classic" examples of FAPs in vertebrate neuroethology—the prey-catching behavior and the advertisement call perception in anurans—are discussed. The conclusion reached is that the original FAP is not a useful concept, neither in ethology nor in neuroethology, and that the neuroethological concepts substituted (feature detector, command neuron, central pattern generator) should either be abandoned or redefined in terms of neuronal network theory.

THE CONCEPT OF "FIXED ACTION PATTERN"
("ERBKOORDINATION")

In 1937–1939, Konrad Lorenz developed the concept of "fixed action pattern" (FAP) in collaboration with Niko Tinbergen (Lorenz 1937a, b; 1939). According to this concept, behavior consists of stereotyped sequences of action ("Erbkoordination," also called "Instinkthandlung" or "Instinktbewegung") that are usually released by specific environmental stimuli in contexts that are highly relevant for survival and/or reproductive success of the individual and that differ only in intensity and velocity. FAPs were originally conceived to be strictly genetically determined or "inborn," although Lorenz later admitted the possibility that FAPs could contain "pieces" of learned behavior ("Instinkt-Dressur-Verschränkung"; Lorenz 1961/1965).

According to Lorenz, each FAP is driven by a particular "action-specific energy" that is continuously produced inside the nervous system and is "consumed" during the occurrence of the FAP or its final component ("consummatory act" or "Endhandlung"). This results in observable changes in the readiness of the animal to perform...
an FAP ("behavioral threshold"). If a FAP is prevented from occurring, e.g., because of lack of an adequate releasing stimulus, it may eventually take place in the complete absence of such a stimulus ("vacuum activity" or "Leerlaufreaktion"). Lorenz’s idea of "action-specific energy" was strongly influenced by Erich von Holst’s concept of "central nervous automatisms," which also gave rise to the concept of "central pattern generator" discussed below.

Under normal conditions, a FAP is thought to be elicited by specific external stimuli called "key stimuli," "sign stimuli," or "releasers" ("Schlüsselreize" or "Auslöser"). Many of these are "social releasers" such as stereotyped gestures or visual, auditory, olfactory, or other signals, e.g., spots on the body, mating calls or sexual pheromones, or features of other animals, such as enemies. Sign stimuli are assumed to affect an "innate releasing mechanism" (IRM; "angeborener Auslösemechanismus") which, in turn, elicits the FAP, provided that sufficient action-specific energy has been accumulated. In ethology, the degree to which this IRM is really "innate" or partly modifiable by experience has been a subject of long debate.

According to Lorenz, Tinbergen, and co-workers, the actual occurrence of a FAP is characterized by the "principle of dual quantification" ("Prinzip der doppelten Quantifizierung"), i.e., by the effectiveness of the sign stimulus/releaser and the actual behavioral threshold, which in turn is determined by the level of action-specific energy. This means that at a high behavioral threshold (or low motivational state), only a very effective sign stimulus is capable of eliciting a FAP, while at a very low behavioral threshold (or high motivation), a relatively "weak" sign stimulus is able to elicit a FAP. Thus, the effectiveness of the sign stimulus and the internal readiness of an animal for a given FAP are two independent variables.

**FURTHER DEVELOPMENT AND CRITIQUE OF THE ORIGINAL FAP CONCEPT**

The FAP concept was severely criticized by a number of American and English behaviorists, who attacked Lorenz's rigid distinction between innate and acquired components of behavior (e.g., Lehman 1953; Hinde 1956, 1966; Thorpe 1963). In particular, the dichotomy between "innate" and "acquired" was considered artificial because these two notions can only be defined by mutual exclusion, i.e., "innate" is everything that is not "acquired" and vice versa.

By contrast, in German-speaking countries the FAP concept was widely accepted and indeed defended by ethologists such as L. Eibl-Eibesfeldt (1967), P. Leyhausen (1968), and K. Immelmann (1976). It must be noted, however, that these authors often made substantial changes to the original concept without proper acknowledgement. A more cautious position was taken by the American ethologist and former student of Lorenz, George Barlow, who proposed to replace the notion of FAP by the more neutral term "modal action pattern" (MAP) and to avoid labels such as "fixed," "instinct," "innate," and "hereditary" (Barlow 1968, 1977). For Barlow, a MAP is a purely descriptive term for a "recognizable spatiotemporal pattern of movement" that cannot be further subdivided into entirely independent-occurring subunits, "although some of its components may occur independently or in other MAPs." They are widely distributed in a similar form throughout an interbreeding population (Barlow 1977). Barlow thus recognized the possibility of a complete continuum between highly stereotyped and highly plastic behavioral acts and tried to avoid any speculations about "underlying" physiological mechanisms.

Recently, a careful analysis of the original FAP theory and its derivatives was published by the German ethologist, Hanna-Maria Zippellius (Zippellius 1992). Zippellius’ criticism is based on the following main arguments:

1. The FAP theory is partly inconsistent in itself and partly circular.
2. Far-reaching statements are made on a largely insufficient and partially incorrect or misinterpreted empirical basis.
3. No serious attempts were made by the founders or their followers to test the crucial arguments of the theory; rather, those results of their own experiments, which were inconsistent with the theory, were either ignored or distorted until they fitted the predictions.
4. Inconsistent results and weak evidence were made increasingly consistent and significant from textbook to textbook by the Lorenz school, without any further empirical investigations.

Of particular importance is the reevaluation of the much-cited "crucial" experiments that formed the basis of the FAP theory. Here we mention the pecking response of nestling herring gulls, the identification of competitors and gravid females by the male stickleback (as the standard example for sign stimuli), and egg identification in the herring gull (as the standard example for "overnormal" sign stimuli). Apart from substantial methodological and statistical deficits, which may be tolerated from a historical perspective, a careful evaluation of the original articles reveals that the results are mostly inconsistent with the conclusions. For example, no truly significant results were obtained with respect to the claimed preferences for the famous red spot on the bill of the herring gull or for the giant artificial egg (rather than the bird’s own clutch) or the swollen vent of the female stickleback. All later experiments on the food-begging behavior of herring gull nestlings came to the conclusion that these animals have no inborn schema of their parents in this context, but learn through trial and error. For other telling examples of experiments crucial to the Lorenz–Tinbergen FAP theory, the reader is referred to the book by Zippellius (1992).

In general, most of the empirical material for the FAP theory appears to have been "made up," either consciously or unconsciously, by Lorenz and his followers. This holds particularly true for the examples cited in favor of the existence of "vacuum activity," e.g., Lorenz’s hand-raised starling, an example that developed through the years from a pure anecdote to a firm proof of the existence of vacuum activity in the context of feeding behavior (for details, see Roth 1974; Zippellius 1992). Despite these
weaknesses, which were known for a long time, hardly any criticism of Lorenz's concept of instinctive behavior or mention of experiments that cast doubt on this theory can be found in a number of recent ethology textbooks (Eibl-Eibesfeldt 1967; Immelmann 1976; McFarland 1985/1989).

THE FATE OF FAP THEORY IN NEUROETHOLOGY

A characteristic of the original FAP concept is that it was developed without any reference to (neuro-)physiological mechanisms. This is particularly true for the mystical “action-specific energy” that was thought to accumulate inside the nervous system and for which no neurophysiological or neurochemical correlate has ever been found. Despite this fact, the FAP concept has thoroughly influenced the field of neuroethology, i.e., the analysis of the neural basis of behavior. Some “founders” of neuroethology, like G. Hoyle, went so far as to define neuroethology as the empirical verification of FAPs in the central nervous system (Hoyle 1984). While this elicited a storm of protest from neuroethologists, it was primarily Hoyle’s idiosyncratic restriction of neuroethology to experiments with “large insects” (Hoyle’s own subjects of research) that was attacked, whereas his rather orthodox definitions of FAP and neuroethology went unquestioned. Current textbooks on neuroethology (e.g., Ewert 1976/1980; Young 1989) refer extensively to the original FAP concept.

In neuroethology, the genuine FAP concept was substantially altered by mixing it with three other concepts: the feature-detector concept, the command neuron concept, and the central pattern generator concept.

Object recognition was thought to be achieved by the action of “feature detectors,” i.e., neurons that respond selectively to particular objects or classes of objects, filtering out all others. The response properties of such detector cells were thought to resemble the prey preferences of the behaving animal closely. H. Barlow (1953) was among the first to develop the feature-detector concept. From the response properties of retinal “on-off” cells in the frog, he derived the existence of a “fly detector” and concluded that through this type of retinal ganglion cell, the retina acts as a filter rejecting unwanted information and passes useful information (Barlow 1953), a view that was later expanded by Lettvin, Maturana, and co-workers (Lettvin et al. 1959; Maturana et al. 1960). This concept was also applied to a number of olfactory, auditory, and visual recognition processes such as sex pheromone identification in moths, mate song recognition in crickets, prey echo location in bats, and prey recognition in toads. It was seen as the verification of Lorenz’s innate releasing mechanisms (Ewert 1976/1980).

The term “command neuron” or “command cell” was introduced by Wiersma and Ikeda (1964) to describe neurons in the crayfish that elicit rhythmic movements of small abdominal appendages, called swimmerets. The concept implies that the activity of one nerve cell, or of a small number of cells, could elicit a complete behavioral pattern. This concept quickly gained acceptance in neuroethology, particularly among invertebrate neuroethologists, “because it provided an elegant neural mechanism to ‘explain’ the release of fixed action pattern by specific stimuli” (Kupfermann and Weiss 1978). Particularly intriguing was the combination of the above-mentioned detector neuron concept with the command neuron concept: “One could envision the nervous system as composed of sensory analyzers that provide an input to a command neuron when themselves excited by the appropriate sensory input . . . . When sufficiently excited, the command neuron fires and in turn excites a neural network that is interconnected so as to produce a complex response appropriate to the sensory input” (Kupfermann and Weiss 1978).

Originally, a central pattern generator was defined as a neural network responsible for the production of the timing cues of a rhythmic motor output pattern in the isolated central nervous system similar to that of the intact animal (Wilson 1961; Bässler 1986). The inputs from the sense organs (e.g., from wings, limbs) were thought to exert only a tonic excitatory input.

While these mechanisms were seen as neural verifications of FAP or parts of it, it became clear that (a) the respective concepts were not as well defined as the FAP concept itself, (b) different authors attributed different meanings to these notions, and (c) their empirical basis was weak or equivocal.

As to the feature-detector concept, it has turned out that in most cases object recognition is not the result of the activity of single detector cells but of neuronal networks; these range from local assemblies, composed of neurons with overlapping response properties, to networks that are widely distributed throughout the central nervous system. Even in the cases most often cited in favor of the feature-detector concept—such as the lobula giant movement detector cells of the locust studied by Rowell and co-workers (cf. O’Shea and Rowell 1977), which set off escape jumping and the low-, high-, and band-pass filter thoracic neurons in the cricket as studied by Huber and co-workers (cf. Huber 1978)—there seems to be no universal agreement among invertebrate neuroethologists as to whether the FAP and/or the feature-detector concept in its rigid sense can be applied.

The same holds for the command neuron and the central pattern generator concept. To date, no “true” command neuron or command system has been identified that unequivocally satisfies the criteria set by Kupfermann and Weiss (1978), which would involve a demonstration that a neuron or small set of neurons is necessary and sufficient for eliciting a complete behavioral response. This does not exclude the possibility that there are cases that come close to the command neuron/system concept, e.g., some individual neurons or small groups of cells in Aplysia (cerebral to buccal interneurons or CBI neurons), the conjoint activity of which drives consummatory feeding responses (Kupfermann et al. 1991). The ecdlosion hormone as a releaser for exoskeleton shedding in the moth, studied by Truman and co-workers (Truman 1992), seems to be a good example for a highly stereotyped behavior that is released by a single hormone acting upon neurons in the abdominal central nervous system. In this context, the telostostal startle behavior mediated by the Mauthner neuron is a vertebrate example and has been much debated. (Diamond 1971; Young 1989). However, this
and other behaviors cited in this context fulfill all of the requirements of a reflex but not of a FAP, which was sharply distinguished from reflexes by Lorenz.

Finally, as to the central pattern generator concept, research over the last ten years has revealed the essential role of phase sensory inputs in the generation of a rhythmic output pattern (Altman 1992). Furthermore, in invertebrates as well as in vertebrates, very little is known about the nature of the central pattern generator, and there is evidence that the motor neurons, rather than representing mere final output stages, may be integral parts of the oscillating network, as is true for sensory feedback pathways (Altman 1992). Under certain conditions, a central pattern generator may not be behaviorally distinguishable from a chain reflex (Bässler 1986). Finally, the central pattern generator concept per se is of little use for invigorating the FAP concept because it is restricted to rhythmic behavior. Also, one can ask whether this concept can reasonably be applied to a premotor system that consists of at least one thousand neurons, such as that found in the Xenopus embryo (Arshavsky et al. 1993).

TWO ALLEGED EXAMPLES OF FAP IN VERTEBRATE NEUROETHOLOGY

To substantiate our critique of the FAP concept and its application in neuroethology, we present two types of vertebrate behavior that are considered the best realizations of FAPs in vertebrate neuroethology: the prey-catching behavior of anurans (particularly of the toad Bufo bufo), as presented by J.-P. Ewert and co-workers, and the advertisement call production and identification in frogs, as studied by R.R. Capranica and co-workers.

In his most recent review article, Ewert (e.g., 1989) makes extensive reference to the FAP concept. For Ewert, prey capture in the toad is a true FAP, i.e., a stereotyped behavior based on a genetically determined neural substrate, although some parts can be modified by experience. Prey objects are identified by an inborn prey recognition system, which consists of a network that includes certain types of retinal ganglion cells (R2, R3, R4), one type of thalamic/pretectal neurons (THS), and several types of tectal neurons (T 5.1, 5.2, 5.3). According to Ewert, the tectal T 5.2 neurons fulfill all requirements of a “feature-detector” because their response properties are claimed to resemble strongly the prey preferences of the behaving animal. The corresponding key stimulus is the configurational property of elongated (“wormlike”) prey objects, i.e., the geometric relationship between elongation parallel and perpendicular to the axis of movement: the more “wormlike” the better. The T 5.2 neuron is not a command neuron in the strict sense of Kupfermann and Weiss, because the simultaneous and consecutive activity of a number of other types of tectal neurons are required for the occurrence of orienting, approach, and snapping. Instead, the T 5.2 neuron is a necessary member of this ensemble and is accordingly called a command element that “tells” the nervous system: this object is a prey! In the tectum, it integrates the prey recognition network and acts as the dominating tectal output cell in the context of prey capture.

Is Fixed Action Pattern a Useful Concept?

Although Ewert and co-workers concentrated on the toad, they always argued that these findings were a general model for feeding in amphibians. There is, however, a substantial amount of data showing that this concept, even in its most recent version, is neither applicable to the toad nor to any other amphibian. Our major points of criticism are:

1. The prey-catching behavior of frogs or salamanders is by no means a stereotyped type and is therefore not a FAP (Roth 1987). Electromyography and high-speed video registrations, either alone or in combination (for frogs, see Deban and Nishikawa 1992; Nishikawa and Gans 1992; for salamanders, see Thexton et al. 1977; Larsen et al. 1989; Miller and Larsen 1990), demonstrate that both frogs and salamanders are able to project their tongues in various directions, at various distances, and at various speeds, and very often do so. Furthermore, amphibians exhibit different feeding “strategies” when confronted with different types of prey (e.g., with or without forward lunge of the body; with or without use of mandibles; see Roth 1987). Finally, prey capture is not “automatically” elicited by a sign stimulus; rather there seem to be many visual features of a prey object that are capable of, either alone or in combination, of eliciting feeding: size, configuration, surface texture, motion, movement pattern etc. (Dicke and Roth, in prep.).

2. There is no close correspondence between the behavioral preference of the toad and the activity of the T 5.2 neuron: the toad prefers 2 x 16” or 2 x 32” (truly “wormlike”) dummies, while the neuron responds best to 2 x 8” dummies, and the behaviorally best stimulus occupies only the fifth and sixth “rank” in the T 5.2 preference. The attractiveness of square stimuli is not significantly different from that of wormlike ones. In addition, T 5.2 neurons respond with equal discharge rate to a number of wormlike and square and even “antiwormlike” stimuli, as can be clearly seen in Ewert’s own diagrams (see, e.g. Ewert 1989, p. 70), and therefore cannot act as reliable feature detectors. Also, this cell (as all visual cells) responds only to angular size, while the toad clearly shows size constancy, i.e., it does not confound small but nearby objects with large but distant ones subtending the same visual angle. Finally, many amphibians neither prefer wormlike prey nor do they possess T 5.2-like neurons (Roth 1987).

3. So far, neither the T 5.2 neuron nor any other tectal neuron could be identified as true command element neurons. Rather, in amphibians as well as in all other vertebrates prey recognition is achieved by means of the interaction of several to many visual neurons, which respond in an overlapping manner differently to various object features. This ensemble of neurons “represents” different aspects of the object (e.g., its configuration, velocity, contrast, movement pattern). In addition to the object identification system, the depth perception system plays an important role since it yields decisive information about absolute size and thus about enemy-prey discrimination. These systems do not seem to converge inside the tectum but may be processed in a parallel manner down to the premotor and motor system (Dicke and Roth 1994).
Amphibian feeding behavior, therefore, cannot reasonably be interpreted as being elicited by key stimuli/feature detectors and as a “fixed” action pattern guided by command neurons or command neuron elements.

The perception of mating or advertisement calls by anurans is seen by many ethologists and neuroethologists as another outstanding example of the existence of a FAP and of sensory processing of key stimuli (Capranica 1983; Capranica and Moffat 1983). The basic concept, as developed by Capranica and co-workers, was that the mating call of anurans is a highly stereotyped, species-specific signal that is detected by the “receiver,” (i.e., a conspecific male or female) through a system of matched filters. In the case of the green treefrog, Hyla cinerea, the energy spectrum of the call is bimodal: it has a peak around 1000 Hz and a second peak of equal amplitude of 3200–3300 Hz. The inner ear of Hyla, like that of most other frogs, possesses two specialized auditory organs: the amphibian papilla and the basilar papilla. The amphibian papilla is innervated by low-frequency, so-called inhibitory, fibers with best excitatory frequencies below 550 Hz and by mid-frequency, noninhibitory fibers with a frequency range of 600 to 1200 Hz. The fibers innervating the basilar papilla are tuned to frequencies above 1200 Hz. Thus, there seems to be a close matching between the two spectral peaks in the frog’s advertisement call and the frequency range of the fibers originating in the amphibian papilla (at least the noninhibitory fibers) and the basilar papilla. The two papillae seem to act as peripheral filters. In order to detect a species-specific mating call, the auditory centers do nothing but compare the information coming from the auditory periphery with a central template, a “mating call detector.” This detector acts as an “AND gate”: it is activated only when both the amphibian papilla channels for low or middle frequencies and the basilar papilla channel for high frequencies occur simultaneously and with the same intensity.

Recent evidence, however, indicates that even this “classic” example of a vertebrate FAP and key stimulus recognition mechanism has to be abandoned. First, both call production and call recognition are much more variable than previously thought and both demonstrate a clear context dependence (Wells 1988; Kuhn and Schneider 1984; Davis 1987). An example of this is the adaptation of the calling phase to the activity of conspecifics, which results in antiphonal calling (Brzoska et al. 1982; Walkowiak 1988). Changes can also occur in call rate, pulse rate, call duration, and spectral composition of the call, depending on the social context (Wells 1988). Furthermore, the dominant frequency of the calls of some amphibians decreases with an increase in body size, which permits the receiver to estimate the size of a potential competitor. Also, there is a number of different intraspecific calls that are distinguished precisely by frogs—a process for which the peripheral filter concept offers no explanation. Finally, the frog’s own activity and its motivation may influence the calling activity (Walkowiak 1988).

Parallel to these insights into the variability of advertisement or mating calls, Capranica now recognizes that the original peripheral matched-filter concept is inadequate (Capranica 1992). It turns out that anurans use a combination of different parameters (like spectral composition, temporal pattern, and intensity of auditory signals) and that central processing of these parameters is much more complex and occurs in a parallel fashion (Hall and Feng 1987). While some authors consider the thalamus to be an important center for call identification (Hall and Feng 1987), others emphasize the role of the mesencephalic torus semicircularis (Walkowiak 1992). The auditory periphery does not act as a sensory filter detector (rather, it is “permissive” to signals), nor is there a “mating-call detector” in the brain of anurans.

CONCLUSIONS AND SUMMARY

In science, new concepts are as important as new empirical data and new methods. However, concepts are useful only if they are clearly defined, empirically testable (and falsifiable), and open to modifications. In ethology, the original FAP concept has played a destructive role because it fulfilled none of these requirements. Instead, as presented above, it is characterized by internal inconsistencies, ad-hoc explanations, untestable or unfalsifiable parts, invented empirical evidence, and the tendency to explain everything and immunize itself against any critique. It has substantially hindered a careful investigation of animal behavior—particularly for the modification of behavior by individual experience—by trying to save the idea that “innate” behavior is sharply distinguished from acquired behavior. In no case has such a sharp distinction been found; rather, we must accept any kind of relationship between rigid and plastic aspects of behavior. G. Barlow expressed this when he asked: “Is there any reality to MAPs or FAPs? I find it impossible to give an operational definition that is general enough to meet all contingencies. . . . Obviously, there is a continuum. At one extreme is patterned behavior, like locomotion, which varies from moment to moment in harmony with the environment. At the other extreme are precisely patterned movements that are relatively independent of external modulation and may even fit the Lorenzian criteria of the Fixed Action Pattern. There is no boundary” (Barlow 1977 p. 128).

What remains is the fact that many behaviors are easily distinguishable from others as MAPs and may characterize members of a species. The reasons for the existence for such MAPs are unclear to date. The relative stereotypy of MAPs may be caused by (a) a “fixed” genetic program determining the internal apparatus controlling behavior (although there is little evidence that such fixed programs exist; see Greenspan et al., this volume); (b) internal processes of self-organization in the nervous system or the locomotor apparatus that leads to a given attractor state (and a respective basin of attraction) or several of such attractor states among which the organism can switch; (c) imprinting and learning processes or the sameness of environmental conditions. It follows that a MAP may have very different causes acting singularly or in combination. In particular, “genetically determined” does not necessarily imply “fixed.” Rather, behavioral plasticity and behavioral rigidity must have a genetic basis.
Concepts in neuroethology—such as those pertaining to the feature-detector concept, the command neuron/system concept, and the central pattern generator concept—were and still are seen as neural realizations of FAPs. These concepts, however, have turned out to be problematic, both with respect to their definitions and empirical foundation. The feature-detector concept seems to be of no use at all and therefore must be replaced by more advanced models for parallel-convergent sensory processing. The command neuron/system concept may still turn out to be useful in cases of very simple behavior; however, its connection to the FAP concept is inadequate because this is a kind of behavior at which the FAP explicitly did not aim. Finally, the central pattern generator concept has been expanded to such a degree, in order to cope with the many internal and external factors determining rhythmic behavior, that it has lost most of its explanatory power. By no means can it be viewed as a realiziation of purely internally driven behavioral acts, as conceived by the original FAP concept.

We see the further evolution of the theory of neural networks as a fruitful way to overcome the difficulties inherent in the FAP concept as well as in the neuroethological concepts discussed. The notions of key stimulus, innate releasing mechanism, feature detectors, command neurons, and pattern generators have either to be abandoned completely or redefined in terms of the structural and functional organization of small to complex networks (some of which may enclose large parts of the nervous system). These networks are intrinsically plastic and may possess different attractor states (see Freeman, this volume) and, depending on the influence of different hormones, neuropeptides, and transmitters, may "produce" different kinds of behaviors, be they stereotyped or not (Decochar, this volume).

ACKNOWLEDGEMENTS

We thank Drs. Walkowiak (Köln), Wullimann (Bremen), Schlosser (Bremen) and Altman (Manchester) as well as colleagues from the present Dahlem workshop for substantial help and criticism.

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